

numbers reported by other workers, it has been concluded that  $x = 14$  is probably the correct base chromosome number for the genus.

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## HYBRIDIZATION AND INSTABILITY OF YUCCA

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The contention that hybridization is largely responsible for the widespread variability of southwestern yuccas (2,4,9)<sup>2</sup> is supported by the following facts. 1) Cross-pollination is enhanced by the yucca's dependence upon the yucca moth for pollination. 2) Two or more species frequently occur in mixed stands or near each other. 3) The karyotypes of all species are strikingly similar (cf. 1). 4) Inter- and intra-specific pollinations produce equally abundant seed. 5) There is little difference in the degree of relationship and the ability to hybridize. 6) Many variants exhibit specific characteristics of two or more species. 7) Apparent hybrids are frequently more fertile than "typical" species. 8) Progenies of apparent hybrids are composed of two or more types. These facts, however, pertain only to putative hybrids and the conditions favoring hybridization. Although a few garden and artificial hybrids (3,8) have been cited, their characteristics, behavior, and fertility have not been recorded. The present study of artificial hybrids indicates that yuccas are genetically similar and that hybridization among native plants is common.

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<sup>2</sup> Numbers in parentheses refer to Literature Cited.

The seeds of the species involved in the hybrids were collected in the following localities:

*Yucca glauca* Nutt., Grant, New Mexico.

*Yucca elata* Engelm., White Sands National Monument, New Mexico.

*Yucca constricta* Buckl., Big Spring, Texas.

*Yucca schidigera* Roezl ex Ortgies, Riverside, California.

*Yucca arizonica* McKelv., Nogales, Arizona.

*Yucca neomexicana* Woot. & Standl., Kenton, Oklahoma.

The pollinations were made at Riverside, California (9), and the hybrids were grown in the University of California Botanic Garden, Berkeley, California. Specimens of the hybrids are in the University of California Herbarium, Berkeley, California.

#### FERTILITY AND MEIOTIC BEHAVIOR

The percent of  $F_1$  fruit obtained from self-pollinations and the viability of  $F_1$  and  $F_2$  seed are given in Table 1.

The microsporocyte divisions of the hybrids were identical or strikingly similar. Each consistently formed 5 large and 25 small bivalents and exhibited few or no irregularities in either the first or the second division. All tetrads appeared normal, and only 6 percent of the matured grains were abortive.

TABLE 1. PERCENT OF  $F_1$  SELFED FRUIT AND VIABILITY OF  $F_1$  AND  $F_2$  SEED

	Percent germination of $F_1$ seed*	Percent of $F_1$ fruit from self-pollinations*	Percent germination of $F_2$ seed
<i>Y. glauca</i> × <i>Y. elata</i> .....	84	88	86
<i>Y. constricta</i> × <i>Y. schidigera</i> .....	64	72	72
<i>Y. arizonica</i> × <i>Y. neomexicana</i> .....	54	24	68
<i>Y. arizonica</i> × <i>Y. glauca</i> .....	62	32	72

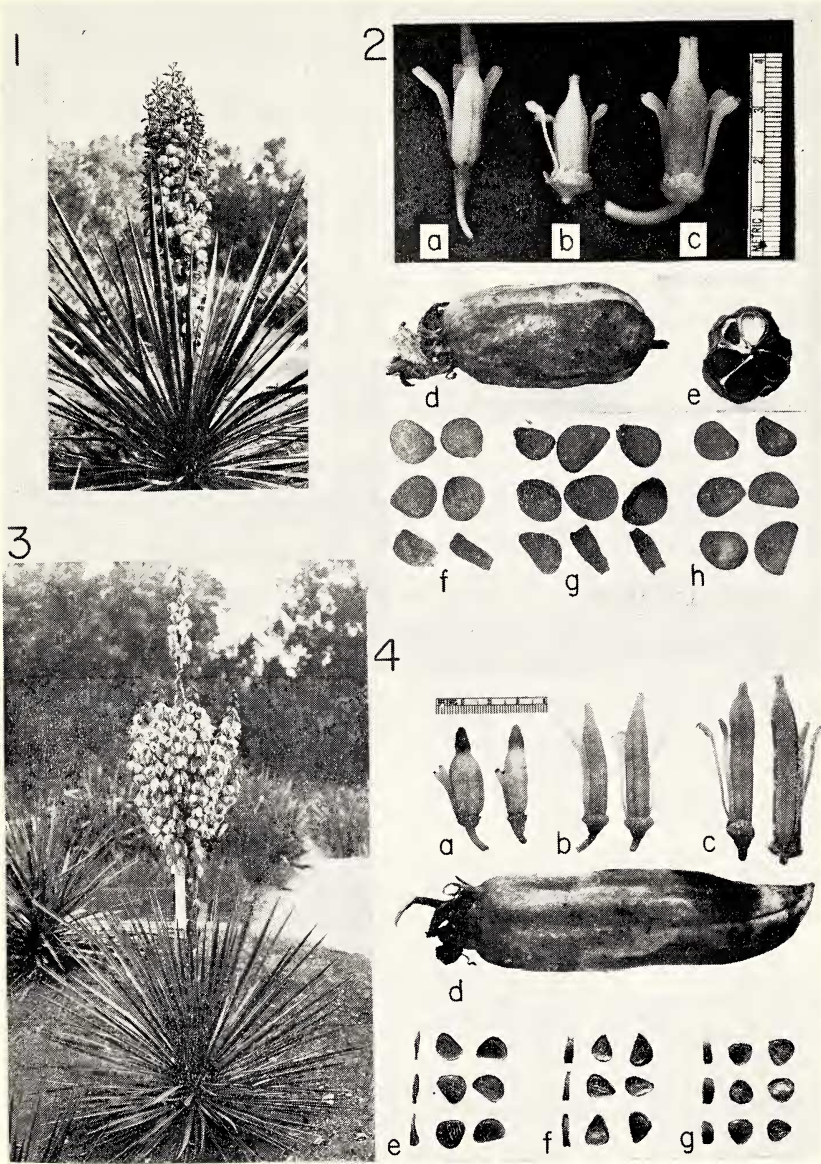
\* Fruit percentages based on 25 pollinations and seed germination based on germination test of 50 seeds.

#### CHARACTERS INDICATIVE OF DERIVATION

The majority of characters of the hybrids are either intermediate in nature or approach those of the parents. The most helpful characteristics in recognizing the derivation of the hybrids are the following:

*Yucca glauca* × *Y. elata*: the low height of the inflorescence (7.05 cm. above foliage) and the greenish, swollen styles approximate those of *Y. glauca*, while the large head of leaves and the paniculate inflorescence resemble those of *Y. elata*. The hybrid is very similar to *Y. intermedia* McKelv. var. *ramosa* McKelv. (5,p.120, pl. 46) and to plants reported possibly to be *Y. elata* × *Y. glauca* hybrids (9, p. 63, pl. 41).

*Yucca constricta* × *Y. schidigera* (figs. 1, 2): the non-fleshy fruit (3.20 cm. thick, 6.35 cm. long) and large, angular seeds (7.20 by 11.1 mm.) are characteristic of *Y. constricta*, while the indehiscent fruit and



FIGS. 1-4. *Yucca* parents and hybrids. FIG. 1. Habit of *Yucca constricta*  $\times$  *Y. schidigera*. FIG. 2. *Yucca constricta*  $\times$  *Y. schidigera* and parents: a, pistil and stamens of *Y. constricta*; b, pistil and stamens of *Y. schidigera*; c, pistil and stamens of hybrid; d, capsule of hybrid; e, cross section of hybrid capsule; f, seeds of *Y. schidigera*; g, seeds of hybrid; h, seeds of *Y. constricta*. FIG. 3. Habit of *Yucca arizonica*  $\times$  *Y. neomexicana*. FIG. 4. *Yucca arizonica*  $\times$  *Y. glauca* and parents: a, pistil and stamens of *Y. glauca*; b, pistil and stamens of hybrid; c, pistil and stamens of *Y. arizonica*; d, fruit of hybrid; e, seeds of *Y. glauca*; f, seeds of hybrid; g, seeds of *Y. arizonica*.

thick, rough seeds containing ruminant endosperm are characteristic of *Y. schidigera*. The only similar fruits found on native plants (9, p.56, pl.34) occurred on plants belonging to the *Y. glauca* alliance, but these fruits contained typical capsular seeds.

*Yucca arizonica* × *Y. neomexicana* (fig. 3) and *Y. arizonica* × *Y. glauca* (fig. 4) are fairly similar. They differ chiefly in the leaf blades being mainly concavo-convex and the flowers globose in *Y. arizonica* × *Y. neomexicana*, while the leaf blades are largely plano-convex and the flowers campanulate in *Y. arizonica* × *Y. glauca*. The most significant features of these hybrids are the following: 1) the non-fleshy, indehiscent fruits and the large, angular, thick, rough seeds containing a ruminant endosperm (fig. 4), which characterize the dehiscent-indehiscent origin of the hybrid; 2) the exceptionally long, conical ovary (3.80 cm.) and fruits (10.3 cm.) (fig. 4), which separate the hybrids from *Y. constricta* × *Y. schidigera* and possibly characterize all hybrids between species of the *Baccatae* series of McKelv. and dehiscent fruit species; and 3) the paniculate-racemose nature of the inflorescence proper (lower half cuneiform, upper half racemose) (fig. 3), which probably characterizes hybrids between plants with typical paniculate and racemose inflorescences. Although no native plants exhibiting the first two of the preceding features have been reported, those with paniculate-racemose inflorescences are fairly common. Such inflorescences are characteristic of *Y. utahensis* McKelv. and *Y. intermedia*, and they are common among native yuccas reported to be possible hybrids (9, pp.56-68, pl.31, 33, 40).

#### YUCCA CONSTRICTA × Y. SCHIDIGERA F<sub>2</sub>

Second generation seedlings of only *Y. constricta* × *Y. schidigera* have been grown. Leaf variations between individuals of a year-old population are as follows: 1.40 cm. wide and 12.0 cm. long to 0.63 cm. wide and 21.3 cm. long; thick, rigid and straight to thin, flexible and falcate; light green to dark green; and thin, entire margin to corneous, denticulate margin. The leaves of several of the seedlings are considerably broader than those of equally as old seedlings of such broadleaved species as *Y. faxoniana* (Trel.) Sarg., *Y. supicola* Scheele, and *Y. gilbertiana* (Trel.) Rydb. Although the seedling leaves of *Y. schidigera* have denticulate margins they become filiferous several months before they are a year old. Corneous, denticulate margins are characteristic of matured leaves in species of the sections *Hesperoyucca*, *Clistocarpa*, and the series *Rupicola* of McKelv.

#### DISCUSSION

The normal meiotic behavior and the high fertility of the hybrids indicate that the chromosomes of the parental species are homologous and differ only with respect to certain genes. Furthermore, since the similar karyotypes of yuccas suggest parallel speciation, it is very likely that there is a considerable degree of genetic affinity between the majority of species. Under these conditions it appears that the major barrier to

interbreeding among the native plants of *Yucca* is spatial isolation. Although these suppositions are supported by putative, natural hybrids involving many species, several species are not included. It is very probable, however, that hybrids involving the latter species have not been recognized, or that barriers other than genetic affinity or geographical separation occur.

The fact that no apparent hybrids involving *Y. schottii* Engelm. have been reported is unquestionably due to the late flowering season of this species. Although similar flowering barriers occur between several other species, usually the flowering period within a group of associated species overlaps. The failure of *Y. arizonica* × *Y. neomexicana* and *Y. arizonica* × *Y. glauca* to fruit freely was probably due to the long style and closed stigma lobes, which commonly prevented fertilization. It is likely that the capitate stigma of *Y. whipplei* Torr. is a structural barrier and that similar barriers exist in other species.

Although dehiscent- and indehiscent-fruited species are frequently associated, no reputed natural hybrids between them have been reported. In general appearance *Y. constricta* × *Y. schidigera* resembles an indehiscent, baccate-fruited yucca, while *Y. arizonica* × *Y. neomexicana* and *Y. arizonica* × *Y. glauca* resemble a capsular-fruited yucca. If these hybrids were admixed with wild plants, they would undoubtedly be considered hybrids between baccate-fruited species and capsular-fruited species respectively. Their true origin could not be determined without careful examination, unless fruits and seeds were available.

The genera *Yucca* and *Agave* have identical karyotypes (6,10) and a similar distribution (1,8,9), and both are highly unstable (1,7,9). Although much of the diversity in *Agave* is attributed to hybridization, considerable is due to polyploidy, mainly allotetraploidy. The polyploids in *Agave* have a wider distribution and, in general, a greater vegetative development than the diploids (1). No polyploids have been reported in *Yucca*. Both thick, succulent-leaved species (*Y. faxoniana*, *Y. torreyi* Shafer.) and thin, flaccid-leaved species (*Y. constricta*, *Y. glauca*) are diploids (6). Furthermore, the distribution of these diploids is as extensive as the combined diploid-polyploid distribution of *Agave*. *Yucca* extends from south-central Mexico to South Dakota (8,9), whereas *Agave* extends from northern South America to Utah and Nevada (1).

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#### REVIEW

*The Physiology of Forest Trees*, a Symposium held at the Harvard Forest, April, 1958, under the auspices of the Maria Moors Cabot Foundation. Edited by KENNETH V. THIMANN with the assistance of WILLIAM B. CRITCHFIELD and MARTIN H. ZIMMERMANN. xvi + 678 pp., illustr. The Ronald Press. New York, N.Y. \$12.00.

Although principles of plant physiology are the same for all forms of plant life, the methods of research will differ depending on what kind of plants are used in experimental work. Truly, it is a great difference in applying plant physiology to cultivated annuals, such as barley or oats on one hand or to forest trees, that may be several hundred years old and many feet tall, on the other. Plant physiologists, working with forest trees have felt for a long time a need for a get-together to discuss their common problems. Dr. Kenneth V. Thimann, Professor of Biology, Harvard University, was responsible for organizing the first International Symposium on The Physiology of Forest Trees. The symposium was held under the auspices of the Maria Moors Cabot Foundation. Over thirty scholars from several European countries, Canada and United States gathered at the Harvard Forest, Petersham, Massachusetts, in April 1957. The topics discussed included: Water relations and sap movement; Photosynthesis; General Biochemistry; Mineral nutrition; Translocation; Root Growth and other phenomena; Photoperiodism and Thermoperiodism; and Reproduction. The papers were edited by Dr. Thimann, with the assistance of Dr. William B. Critchfield and Dr. Martin H. Zimmermann, and published in one volume. Publication of this volume signifies, if not the birth, at least a formal recognition, of a new branch of Plant Physiology.

The import of this book on the further development of Forest Tree Physiology will be felt for a long time.—N. T. MIROV, Pacific Southwest Forest and Range Experiment Station, Berkeley, California.

#### NOTES AND NEWS

ALPHABETICAL LIST OF FAMILIES FOR MUNZ AND KECK. An alphabetical list of families, giving the page on which each family begins, is available for Munz and Keck, *A California Flora*. It is intended for pasting to the inside of the back cover. Copies may be had by sending a request for the number desired, together with a stamped self-addressed envelope, to Rancho Santa Ana Botanic Garden, 1500 North College Avenue, Claremont, California.

Some publications of interest follow:

*Origin of Primary Extraxylary Stem Fibers in Dicotyledons*, by Amélie Blyth. University of California Publications in Botany 30 (2): 145-232, pls. 1-23. 1958. \$1.75.

*Secondary Phloem of Calycanthaceae*, by Vernon I. Cheadle and Katherine Esau. University of California Publications in Botany 29 (4): 397-510, pls. 60-67, 109 figs. in text. 1958. \$2.25.

*Ontogeny of the Inflorescence and the Flower in *Drimys winteri* var. *chilensis**, by Shirley Cotter Tucker. University of California Publications in Botany 30 (4): 257-336, pls. 24-33, 43 figs. in text. 1959. \$1.50.